

FOREST SNAIL FAUNAS FROM S. E. QUEENSLAND
AND N.E. NEW SOUTH WALES (AUSTRALIA):
PATTERNS OF LOCAL AND REGIONAL RICHNESS AND DIFFERENTIATION

John Stanislak¹, Robert A. D. Cameron^{2*}, Beata M. Pokryszko³ & Jeffrey C. Nekola⁴

ABSTRACT

While regional snail faunas of low-latitude regions tend to be richer than similar areas at high latitude, there seems to be little difference between site (e.g. < 400 m²) richness, which often ranges between 20 and 40 species across a wide latitudinal range. Given this seeming paradox, it is surprising how little investigation has been made into how land snail species are packed into the tropical landscape across multiple scales. This paper addresses this question by analyzing faunal lists from six regions spread across a 550 km extent in the temperate rain forests of eastern Australia. Considerable heterogeneity was observed both within similar habitat types within (ca. 40–60% faunal similarity) and between (ca. 10–50%) different regions. The Charopidae constituted the largest fraction of the fauna (up to 70% of species), and were thus responsible for most of the variation in composition. While the number of species per region (ca. 30–50) was broadly comparable to Europe and North America, the rate of faunal turnover with distance was found to be 2–30 times greater. While geographic turnover in European and North American faunas is largely driven by large species, in eastern Australia turnover was largely driven by small, litter-dwelling species that tend to be unique to each region. The comparative richness of the eastern Australian fauna is thus largely related to evolutionary processes that have caused divergence at regional scales, rather than increased niche-packing or syntopic diversity at site scales.

Keywords: terrestrial gastropod, biodiversity, distance decay, evolution, Australia, North America, Europe.

INTRODUCTION

Recent work in many parts of the world has revealed a great variety of regional patterns in land mollusc species richness and differentiation (Barker, 2005; Cameron, 2004; Cameron et al., 2000; Nekola, 2003, 2005; Pokryszko & Cameron, 2005; Seddon et al., 2005; Stanislak, 1994; Stanislak & Ponder, 2004; Tattersfield, 1998.). These studies have tended to show that distance decay in similarity (Nekola & White, 1999) in regional faunas is low at high latitudes (Pokryszko & Cameron, 2005; Nekola, 2005), presumably due to climate fluctuations resulting in widespread extinctions of forest faunas followed by recolonization from relatively few refugia. At lower latitudes, where such widespread extinctions did not occur, patterns are more com-

plex and reflect the interaction of local environmental gradients and history with differences in dispersal abilities and *in situ* speciation rates (Solem, 1984). These processes may allow some groups to display rapid distance decay rates while others demonstrate little. Thus, in semi-arid northwestern Australia, large and relatively stenotypic camaenids generally show dramatic patterns of allopatric replacement, while non-camaenids are ubiquitous (Solem, 1988; Cameron, 1992). In mesic subtropical New Zealand, compositional differences tend to reflect turnover among small, leaf litter dwelling charopid and punctid snails (Barker, 2005) but without clear patterns of allopatry in congeners.

Local-scale community patterns are less well known, especially in tropical and subtropical environments where densities are often low,

¹Queensland Museum, PO Box 3300, South Brisbane, QLD 4101. Australia.

²Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2DL, and Department of Zoology, The Natural History Museum, London, SW7 5BD, U.K.

³Museum of Natural History, University of Wrocław, Sienkiewicza 21, 50-335 Wrocław, Poland.

⁴Department of Biology, MSC03 2020, 1 University of New Mexico, Albuquerque. New Mexico 871131-0001, U.S.A.

*Corresponding author: radc@blueyonder.co.uk

leading to acute sampling problems (Cameron & Pokryszko, 2005). Contrary to Solem's (1984) assertion, we now know that some tropical rainforest faunas are the richest known at 1 km² scales (Emberton, 1995; de Winter & Gittenberger, 1998; Schilthuizen & Rutjes, 2001). At even smaller scales (i.e. 0.1–1 ha), patterns are even more obscured by sampling problems. As many tropical and subtropical forests are oligotrophic and support only very low densities of snails, it is often impossible in such circumstances to distinguish between genuine local heterogeneity and sampling effects. However, such heterogeneity could be significant both for speciation events and for the co-existence of closely related species (Cameron et al., 2003).

The forests of eastern Australia have been extensively surveyed (Stanisic, 1994, 1997; Stanisic & Ponder, 2004). They constitute a complex mosaic of forest types, determined by substrate, temperature and rainfall, with a history of fluctuation in extent and connectedness. Paralleling patterns seen in E. Africa (Tattersfield, 1998; Seddon et al., 2005), individual sites may harbour up to 40 species, with considerable faunistic turnover occurring over relatively short distances. In this study, we attempt to relate local and regional variation in species richness and compositional turnover to broader regional patterns using both new surveys that attempt to overcome problems of sampling efficiency (Cameron & Pokryszko, 2005), and by reanalysis of some of Stanisic's (1997) earlier results.

STUDY AREAS AND HABITATS

Four major study areas were analyzed with multiple samples, while two outlying sites were represented by single samples (Fig. 1). The Macleay Valley in northeastern New South Wales was the subject of a major survey by Stanisic (1997), covering a geographic extent of approximately 10,000 km² (maximum linear distance of 70 km) with an altitudinal range extending from sea level to approximately 1,100 m. As described and referenced by Stanisic (1997), this area contains a wide variety of forest types, including:

(a) Sclerophyll Forests (SF) dominated by *Eucalyptus* species, have been historically exposed to frequent fires. While such forests can be further divided into Wet and Dry types, for these analyses, all have been lumped; both hold very poor faunas (Stanisic, 1997, and see below).

(b) Temperate Rain Forests (TRF) generally occur at high altitudes and have higher yearly precipitation levels. While we have lumped Warm and Cool subcategories together, most sites would fall in the Warm subcategory.

(c) Dry Rain Forests (DRF) occur in isolated patches at lower altitudes, and typically contain *Araucaria* species in the canopy.

(d) Coastal Rain Forests (CRF) supporting a high density of vine or liana taxa.

(e) Limestone outcrops (LO) which frequently maintain either TRF or DRF vegetation in a SF or disturbed land matrix. These sites are usually small and isolated, and provide rocky shelter and high calcium levels needed by a number of species (Stanisic, 1997). The vegetation is protected from fire by rock debris, and may be described as Vine Thicket, in which big trees are absent, but the vegetation is not fire-tolerant.

In 2004, new samples were made in the Macleay Valley in TRF, DRF, and LO. Most of these sites represent repeat sampling of sites used in Stanisic (1997), and are distinguished from these prior samples by being referred to as "Kempsey".



FIG. 1. Locations of study areas (italic upper case) in SE Queensland and NE New South Wales.

The three other major sampling areas were in southeastern Queensland. Samples near Kenilworth were made on the fringes of Conondale National Park in the valley and low hills surrounding the Mary River, with an outlier at Mapleton. Maximum linear extent was c. 10 km (Mapleton, ca. 30 km) with an altitudinal range from 120–250 m. All but one site were in DRF, the exception (site 3) being in Riverine Rain Forest (RRF) with large strangler figs, *Ficus watkinsiana*. Samples from Brisbane Forest, all collected within 10 km of each other, come from patches of Rain Forest near hill summits. All but one site (all above 650 m) were classified as Wet Rain Forest (WRF), the exception (site 5) being in DRF at c. 450 m. Samples from Lamington National Park, in the Border Ranges, fall into two categories: two at approximately 800 m in WRF, and two below 500 m in DRF. All sites are within 5 km of each other. Maximum linear extent (Kenilworth to Kempsey) was approximately 550 km. Two additional samples were made between the most southerly of the Queensland areas (Lamington) and the Macleay valley/Kempsey. At Glenugie, the sample was made in DRF and Vine Thicket on basaltic talus slopes. At Iluka, the sample came from a patch of CRF.

METHODS AND MATERIALS

Details of sampling methods used in the Macleay Valley survey are given in Stanislak (1997). Collections involved both searching by eye and the collection and subsequent searching of litter, but sampling intensity was not uniform between sites. From the sites sampled, we have chosen for further analysis 69 in which the habitat is unambiguously in one of the five categories described above, and in which at least two species were recorded. Sites from “woodland” or in other disturbed or mixed habitats are excluded. These lack many of the species found in less disturbed vegetation (Stanislak, 1997). The set of samples used here nevertheless includes all the native species found in the original survey.

In 2004, sites in the Macleay Valley were selected to be representative of the major habitats described above, excluding SF and CRF. In the other regions examined, sampling

concentrated on the dominant rainforest categories. The area searched varied between c. 400 m² and 1 ha. Searches involved between two and four person-hours. About 10 l. of litter was collected and sieved at each site; coarse material was examined *in situ*, and the remainder was bagged and examined in the laboratory. All identifiable shells were extracted, identified and counted. Some large and easily identified species were counted in the field and left *in situ*.

All identifications were carried out by J. Stanislak or D. Potter. Where morphospecies are recognised, but not yet formally described, they are given a reference number connected to examined and documented lots in the Queensland Museum. Nomenclature of described species follows Stanislak (1997). Lots constituting new locality records are retained by the Queensland Museum with other material deposited in the Museum of Natural History, Wrocław, and in the National Museum of Wales, Cardiff.

Similarities between pairwise combinations of faunas have been analysed using the Nei index, in which the number of species in common is divided by the geometric mean of richness between both faunas. This statistic has a linear relationship to single step changes in similarity (Pokryszko & Cameron, 2005) unlike the familiar Jaccard index (Nekola & White 1999), which is concave. For the Macleay Valley survey, we have also considered similarity as the proportion of common species to the least rich member of the pair, following exclusion of all species recorded only from single sites, as such unique species only add to dissimilarity. In all analyses, we attempt to take sampling error (Cameron & Pokryszko, 2005) into account, chiefly by a conservative approach to the analysis of differences.

We have used Whittaker's Index ($I_w = S/\alpha$, where S = number of species recorded for the region and/or habitat within it, and α = mean number of species per site within that category), and its variant ($I_{max} = S$ divided by the number of species in the richest site recorded), as indicators of faunal differentiation between sites in the same region (Cameron & Pokryszko, 2004). The latter index eliminates the effect of site faunas that are merely impoverished versions of others, rather than containing distinctive species not found elsewhere.

TABLE 1. Basic data for the 69 sites used from the Macleay Valley survey (Stanisic, 1997). Single-tons, species found in only one site overall; Single/habitat, species found only in one site in that habitat. 50%+/habitat, species found in half or more of sites in that habitat.

	SF	TRF	LO	DRF	CRF	Total
Number of Sites	17	22	9	15	6	69
Number of Species	28	55	71	62	27	112
Mean no. of species/site	3.64	7.95	27.9	12.73	9.5	
Standard Deviation	1.5	4.11	6.45	5.14	4.18	
Range of no.s of species/site	2–6	3–17	21–40	5–22	4–14	
I _w	7.69	6.92	2.54	4.87	2.84	
I _{max}	4.67	3.23	1.78	2.82	1.93	
Number of Unique species	3	16	18	11	1	49
Number of singletons	2	10	9	7	1	29
Single/habitat	15	25	21	16	9	
50%+/habitat	0	3	21	3	9	

RESULTS

Macleay Valley Survey

Appendix 1 lists, by habitat, the species-level taxa found among the 69 sites considered. These include all species reported in Stanisic (1997). Details of site locations and faunas are available at the Queensland Museum, or in electronic form from the authors. Table 1 shows the basic data for these sites by habitat. A total of 112 species, including five introduced species (* in Appendix), were found. None of the introduced species were abundant or widespread.

As shown by Stanisic (1997), SF sites have the poorest faunas, and LO the richest. The values of I_w and I_{max} show that recorded SF and TRF forest faunas are exceptionally heterogeneous, while those of LO and CRF are much less so. The high level of heterogeneity among sites is also shown by the high proportion (29 species, 26%) of species recorded from only one site, and by the low proportions of species that occur in at least 50% of the sites in any one habitat. Strikingly, no species occur in more than half of the SF sites, and only in LO and CRF sites are there more than 10% of species in this category. Conversely, 45% or more of species occur only once within SF or TRF sites, while 33% or fewer of species occurred only once in LO, DRF and CRF sites. Among the habitat faunas, only one species is unique to CRF, three to SF, while LO harbours 18. Only 10 species were observed within all five habitats. Of the 41 species missing from LO sites, most are so infrequent (20

have only single reported occurrences) that their absence from limestone sites may be attributed to sampling error, given the small number (9) of observed sites.

Table 2 shows the matrix of similarities between habitats. The Nei index demonstrates that the strongest connection is between LO and DRF, whereas the maximum similarity index identifies that CRF sites are most related to LO and DRF faunas. Both indices strongly indicate that SF faunas are differentiated from CRF and LO.

For the overall fauna, the Charopidae are much more numerous (55 species, 49%) than

TABLE 2. Similarity matrices for between-habitat comparisons in the Macleay Valley using (A) the Nei index, and (B) taking the number of species in common (excluding those recorded once only) as a proportion of those in the poorest habitat (ex unique). Values expressed as percentages.

A: Nei	TRF	LO	DRF	CRF
SF	48	38	48	47
TRF		50	53	44
LO			65	53
DRF				56

B: Ex unique	TRF	LO	DRF	CRF
SF	73	65	77	50
TRF		69	69	65
LO			78	88
DRF				88

TABLE 3. Numbers and proportions of species in Charopidae in Macleay Valley sites, by habitat, by position in the quartiles of overall frequency, and by habitat range (number of the five habitats at left in which the species were recorded). Quartiles differ slightly in size because of ties in frequency. Note that the bottom quartile (4) consists of species recorded in only one site overall.

Charopidae	No.	%	Quartile	Total species	Charopidae	%
SF	8	29	1	30	10	33
TRF	27	49	2	29	12	41
LO	28	39	3	24	13	54
DRF	24	39	4	29	21	72
Total	55	49	Habitats	Total species	Charopidae	%
			1	49	33	67
			2	25	10	40
			3–5	38	12	32

any other family (Table 3). SF has the smallest proportion of charopids in its fauna (8, 29%) while TRF has the largest (27, 49%). Nearly three quarters of all single-site species are charopids, as are two thirds of all single-habitat specialists. This single family thus accounts for most of the observed differences between habitats and among sites within habitats.

2004 Surveys

Appendix 2 lists the 149 species level taxa found by survey area. Six of the species recorded are introduced (* in Appendix). Of these, only *Lamellaxis clavulinus* was recorded in large numbers, and then only in one site. Full details of sites, and of the species composition of samples from each are deposited at the Queensland Museum and are available

electronically. Table 4 shows the basic data for each survey area. Results for Kempsey are split by habitat, as the range of habitats sampled was much greater than elsewhere, and the LO sites are very different from all others. Of the categories with more than one sample, only in Kempsey LO do all sites meet the minimum requirements of at least 10 times as many individuals as species and at least 200 individuals, and in Lamington and Brisbane virtually no site meets these criteria (Cameron & Pokryszko, 2005). Logarithmic rank/abundance curves tend to be concave in Brisbane and in some Kempsey habitats, with a tail of very rare species. They are more convex in Lamington and Kenilworth, where the pattern is very similar to that recorded for non-limestone Carpathian forests in central Europe (Fig. 2). Within the Kenilworth set, there is also

TABLE 4. Basic data for each area in the 2004 survey. Ind/site, mean number of individual shells collected or recorded per site. For habitat abbreviations, see text.

	Kenilworth DRF/RRF	Brisbane WRF/DRF	Lamington WRF/DRF	Kempsey LO	Kemp DRF	Kemp TRF	Glenugie DRF	Iluka CRF
Sites	10	6	4	3	3	1	1	1
Species	49	34	41	51	36	11	18	11
Mean/site	24.1	13.5	22.3	28.0	17.0	11	18	11
SD	4.4	3.2	7.9	1.7	6.2	N/a	N/a	N/a
Range	17–32	9–17	13–32	27–30	10–22	N/a	N/a	N/a
I _w	2.03	2.52	1.84	1.82	2.12	N/a	N/a	N/a
I _{max}	1.53	2.00	1.28	1.70	1.64	N/a	N/a	N/a
Ind/site	295	135	122	3033	136	35	433	248
SD	162	46	51	2911	66	N/a	N/a	N/a
Range	109–558	92–218	72–185	369–6141	60–185	N/a	N/a	N/a

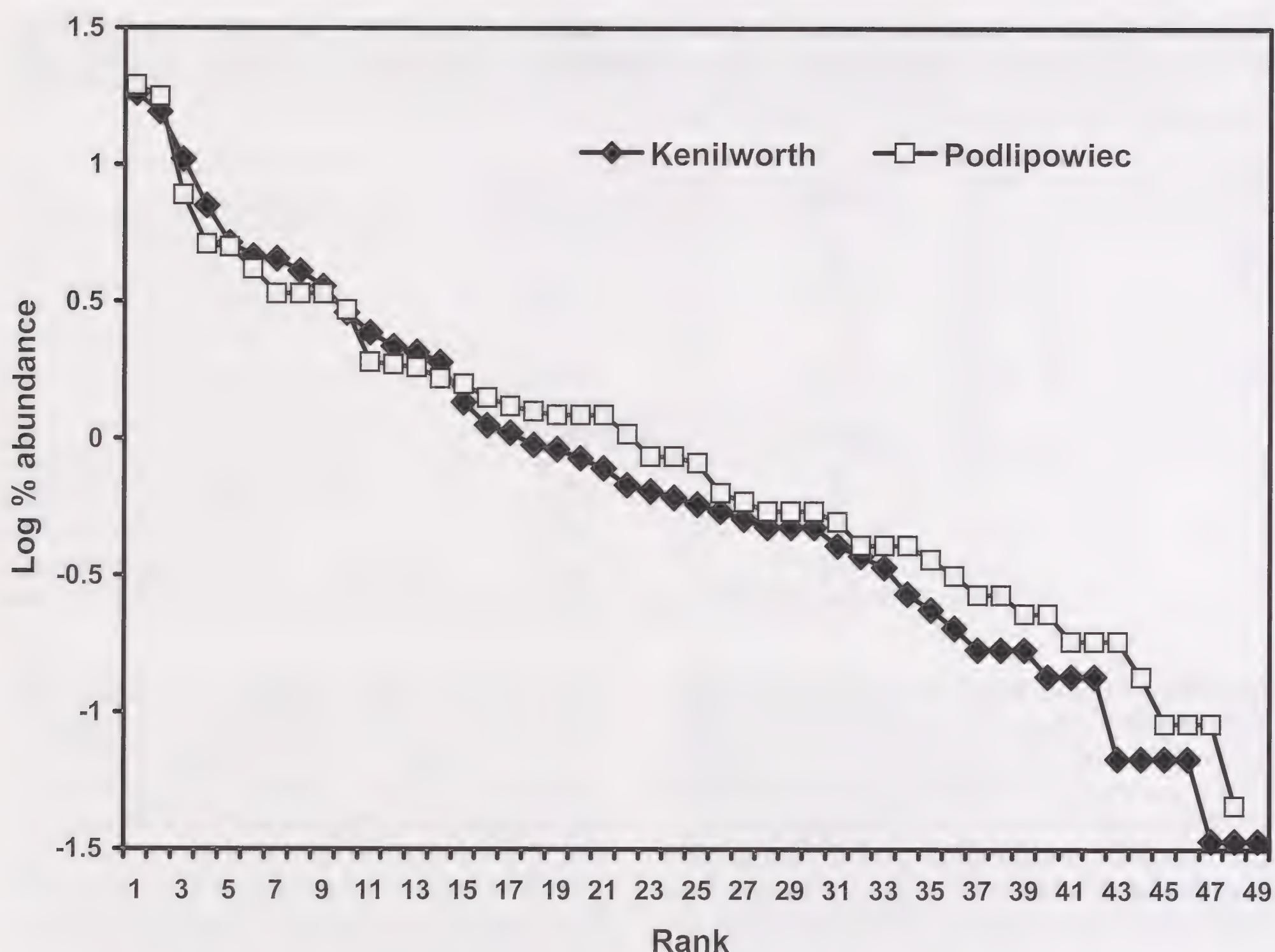


FIG. 2. Logarithmic plot of relative species abundances (%) for the snail faunas in samples from Kenilworth, Queensland, and from Carpathian beech forests at Podlipowiec, S. Poland (Pokryszko and Cameron, unpublished).

no significant correlation between numbers of species and of individuals ($R = 0.22$, $P > 0.2$, $n = 10$). Thus, with that exception, we may suspect that recorded site faunas are significantly incomplete. Nevertheless, the range of site richness, and the values of I_w and I_{max} are generally much lower than those seen within habitats in the Macleay survey.

These indices are larger in Brisbane than elsewhere. In this area, five of the six sites are characterised as WRF, all above 650 m asl. The other site, DRF at c. 450 m, harbours six unique species, and is one of the two richest sites across the entire survey. Without this site the WRF sites of Brisbane have a mean of 12.8 species/site and I_w and I_{max} values of 2.19 and 1.64 respectively, more in line with values for other areas. A similar pattern is evident at Lamington, where the two lower elevation DRF sites (with *Araucaria*) were richer in species and individuals than the two higher elevation WRF sites. Because of limited number of samples, however, not enough statisti-

cal power exists to test hypotheses regarding this pattern. At Kenilworth, one site (Kenilworth 3) comes from Riverine Rain Forest, but shows no peculiarity in richness or native species composition from the remaining DRF sites, though it contained large numbers of the introduced *Lamellaxis clavulinus* (Subulinidae).

Charopidae are the most numerous family in terms of species. As in the Macleay survey, they generally contribute to differences (rather than similarity) between areas, except in the single-site cases of Glenugie and Iluka. Omitting these two, the overwhelming majority of species are found in only one region, and only three (2.1%) are found in all four.

Table 5 shows Nei similarity index values within and between regional habitat and total faunas. Fig. 3 shows the dendrogram of similarities between sites generated by UPGMA clustering. The Kenilworth faunas are the most uniform, with an average inter-sample similarity of 64% in the region. Strong distance

TABLE 5. Values of the Nei index of similarity (%) in the 2004 survey, A: on mean site-by-site comparisons within and among areas and habitats; B: among the total faunas of each area.

A: Nei, mean	Kenilworth	Brisbane	Lamington	Kempsey DRF	Kempsey LO	Kempsey TRF	Glenugie	Iluka
Kenilworth	64	32	20	5	6	6	13	8
Brisbane		55	44	12	9	21	14	6
Lamington			55	11	4	16	6	5
Kempsey DRF				40	29	30	9	4
Kempsey LO					51	20	14	17
Kempsey WTRF						n/a	14	9
Glenugie							n/a	22
Iluka								n/a

B: Nei, total	Brisbane	Lamington	Kempsey	Glenugie	Iluka
Kenilworth	52	34	18	14	29
Brisbane		51	17	21	10
Lamington			13	12	5
Kempsey				15	15
Glenugie					22

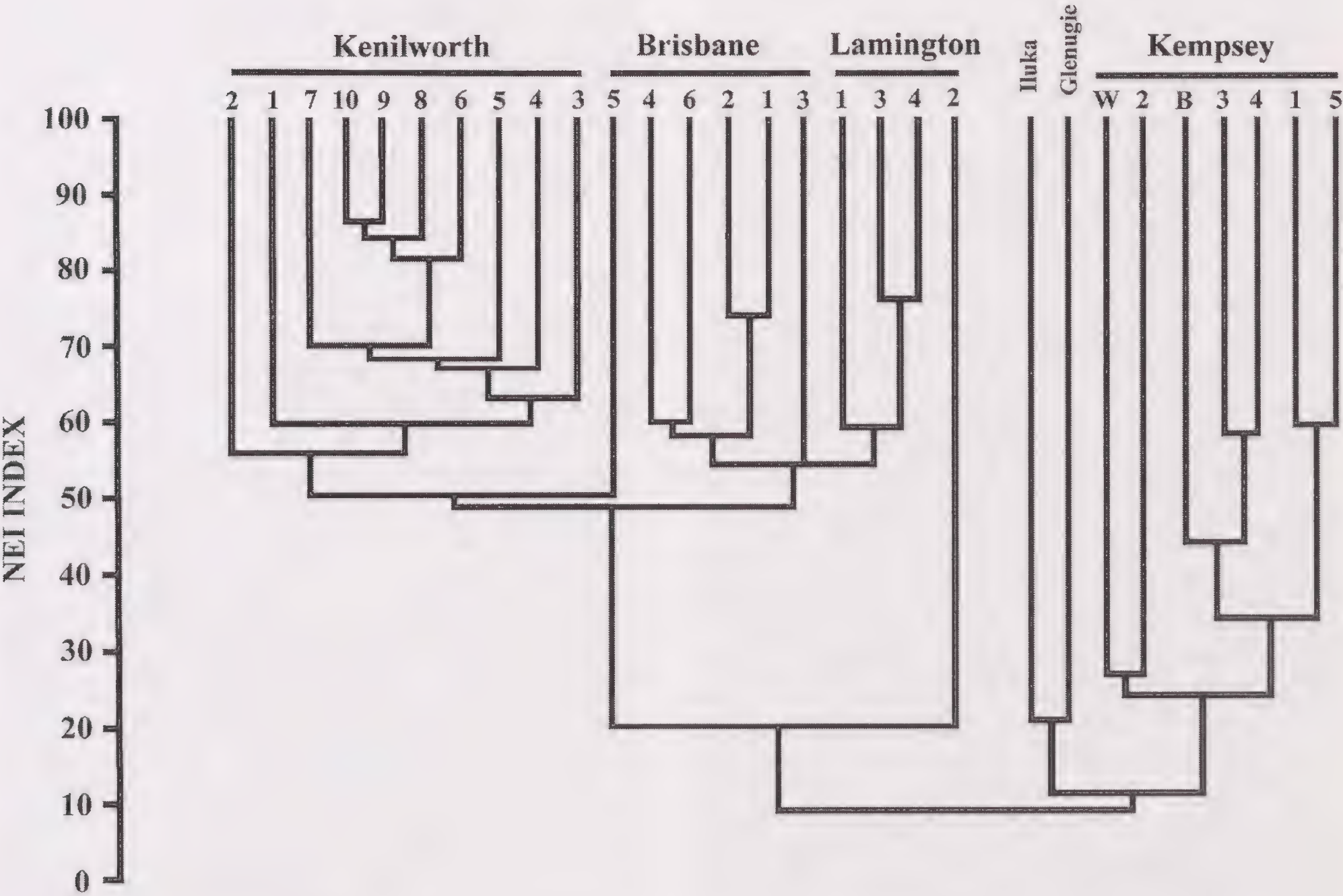


FIG. 3. Dendrogram of Nei index similarities for 2004 study sites (UPGMA). In Kempsey, sites 1, 4 and 5 are from limestone outcrops; W (WayWay Forest) and B (Bob’s Road) are based on very small samples (see text).

TABLE 6. A comparison of the numbers of species found in the original Macleay Valley survey and in 2004 for six sites (see text). Kempsey 4, 1 and 5 are limestone sites, 6 and 7 are DRF, 2 is TRF.

Species	Natural Arch Kempsey 4	Yessabah Kempsey 1	Mt Pleasant Kempsey 5	Blowhole Kempsey 7	Way Way Kempsey 6	Bob's Rd Kempsey 2
Macleay (JS)	35	40	32	14	22	8
2004	30	27	27	19	10	11
Present both	25	25	21	12	9	6
Aggregate	39	42	36	21	23	13
Nei index (%)	78	76	74	74	61	64

decay is apparent between regional faunas, with only 6% similarity being noted over the 550 km extent from Kenilworth to Kempsey. All Queensland areas have low affinities to New South Wales areas (4–16%), while similarity between New South Wales sites also are surprisingly low (4–22%). While the dendrogram also generally demonstrates this same pattern, it also shows that the Brisbane DRF habitat resembles Kenilworth DRF sites. Thus, all six species unique in the Brisbane area to this single DRF site are held in common with one or more Kenilworth DRF sites.

The comparison of total study area faunas may provide more robust results by summing across multiple samples, increasing the number of encountered microenvironments and individuals (Nekola & White 1999). Similarity patterns for total faunas at this scale demonstrate essentially an identical pattern, with similarity falling to 14% between Kenilworth and Glenugie. Similarity of Kenilworth and Kempsey non-limestone sites fell to 6.3%. While Queensland sites maintained somewhat higher similarities (34–52%), inter-area similarity south from Lamington generally ranged from 12 to 15%. The least similarity was noted between the faunas of Lamington and Iluka (5%). Thus, the New South Wales sites are equally dissimilar to each other as they are to the Queensland areas. This can be explored in more detail (Table 4). With the exception of Brisbane, roughly mid-way between Lamington and Kenilworth, more than 40% of recorded species were unique to each region. The highest proportion of unique species (78%) was observed at Kempsey. While this may represent the presence of base-rich limestone habitats, geographic factors also appear important as the frequency of unique species within the Kempsey non-limestone fauna remains significantly higher (68%) than that observed from all other sites.

Macleay- Kempsey Comparisons

Six of the seven Kempsey sites sampled in 2004 had been visited in the earlier survey. A comparison of results is thus possible (Table 6). Although areas searched do not exactly correspond, the differences between occasions show that even when sample sizes are large (Kempsey 1 produced more than 6,000 shells), not all the fauna is necessarily detected. Nevertheless, indices of similarity for repeat samples at the same site are higher than those generally recorded between sites in the same habitat. It is clear that one sample, Kempsey 6, Way Way Forest, was seriously deficient in 2004, with only 60 individuals and 10 species retrieved. This is reflected in its distant relationship to all other sites in Figure 2. Using the combined data for each Kempsey/Macleay site increases levels of between site similarities within each habitat (data not shown). The combined total numbers of species in each of these sites match the maxima for those habitats recorded in the earlier survey quite closely. Overall, the 2004 survey recorded only 67 species in Kempsey, or 60% of those recorded in the larger Macleay Valley survey. As the two habitats not examined in 2004, SF and CFR, hold few unique species, thus lower number mainly reflects the smaller number of samples made and the smaller proportion of the original survey area sampled. While the earlier Macleay survey clearly gives a more comprehensive view of the fauna of each habitat, it does not identify much different rates of turnover with other faunas. For example, similarity between DRF in the 1997 Macleay survey and Kenilworth provided a Nei Index of 16.7% versus 18% for the 2004 Kempsey data. Deficiencies in sampling are thus not seriously distorting similarity estimates between faunas.

DISCUSSION

Reliability and Sampling Error

It is clear that in both the 1997 Macleay Valley and 2004 Kempsey surveys, site faunas were incompletely inventoried (Cameron & Pokryszko, 2005), largely due to the low densities of individuals on non-limestone sites. As shown by the very high values of I_w , I_{max} , and the large proportion of singleton records, this problem was most acute in the 1997 survey, with some of this error reflecting variation in sampling intensity between sites. In the 2004 standardised surveys, this problem remained, but was less severe. Only Kenilworth and Kempsey LO sites were adequately sampled based on total observed richness and abundance (Cameron & Pokryszko, 2005). However, comparisons with the 1997 survey in Macleay/Kempsey suggest that even samples of approximately > 6,000 shells may not completely inventory all taxa, or that very small shifts in location may add more species to an inventory, even within the same habitat. The logistics of quadrupling sampling effort at each site are likely impossible within reasonable time frames. In spite of these limitations, 2004 site data compare favourably with most other tropical studies (Emberton, 1995; de Winter & Gittenberger, 1999; Schilthuizen & Rutjes, 2001), and are similar to those recorded by Tattersfield (1996) in Kakamega Forest, Kenya, where supporting evidence suggests that the aggregate fauna has been adequately inventoried (Cameron & Pokryszko, 2005; Tattersfield et al., 2006). The possible effects of such sampling error on diversity estimates are considered below where relevant. Compared to the traditional Jaccard index, the Nei index of similarity gives some compensation for differing richness in compared sites. Estimates (data not shown) based on the proportion of species held in common by the poorer of two sites shows the same pattern as that revealed by the Nei index. Since we are more concerned with faunal differences, than with richness *per se*, we have refrained from using rarefaction or species accumulation curves, as these give no indication of which taxa might have been overlooked.

Habitat Effects and the Range of Local Richness

Stanisic (1997) demonstrated in the Macleay Valley that SF was the least rich at site level,

while LO was the richest. Our 2004 surveys replicate that finding, and allow estimation of maximum richness levels for each habitat studied. At the site level, LO site maxima exceed 40 species. That the total fauna of LO sites is considerably higher in the original 1997 (71 species) and in the more limited 2004 survey (51 species) reflects both environmental differences between LO habitats and the presence of single outcrop endemics (Stanisic, 1997). Using data from both 1997 and 2004 where possible, DRF off limestone have maxima of 22–23 taxa/site, TRF and CRF have maxima from 15–17, while SF has a maximum of 6. SF and CRF, both base-poor habitats, appear to simply harbour reduced versions of the faunas found in base-rich habitats, as they support very few unique species, most of which are known from only single records. While more intensive work might raise these maximum richness figures slightly, it seems likely that greater between-site heterogeneity in base-poor habitats reflects a genuine patchiness in species distributions at scales larger than sample sites. We cannot tell at present whether this heterogeneity reflects small-scale geographical differentiation within the valley.

In the Queensland series, evidence suggests that WRF supports less rich faunas as compared to DRF, especially in Brisbane and Lamington. For WRF, richness appears to range up to 25 per site, and to 35 over larger areas of a few km². However, DRF can support more than 30 species in single sites both in Lamington and Kenilworth, while they appear to range up to 40–50 over larger areas.

These local richness levels are similar to those found in forest faunas from tropical East Africa (Tattersfield et al., 2006; Seddon et al., 2005), but the maxima are rather less than those found on the North Island, New Zealand (up to 64 in a site, perhaps 75+ in a few ha, Barker, 2005). While rainforests in Madagascar, Cameroon and Borneo are richer at larger scales (60–110 species per 1 km²; Emberton, 1995; de Winter & Gittenberger, 1998; Schilthuizen & Rutjes, 2001), at the scale of 400 m² plots accurate comparisons are not possible due to sampling errors (Cameron, 2004; Cameron & Pokryszko, 2005). Surprisingly, the range in site richness values is remarkably similar (2–45 species/site) to that recorded in European (Pokryszko & Cameron, 2005) and eastern North American (Nekola & Smith, 1999; Nekola, 2005) temperate forests. Thus, maximum site richness of forest faunas shows little global latitudinal variation, despite

great and deep taxonomic differences. This observation also holds more generally within eastern Australia, where sites holding c. 35–40 species can be found at widely separated latitudes (Stanisic, 1994; Stanisic & Ponder, 2004).

The pattern in all four of our study areas seems to conform to Waldén’s (1981) conclusion that within a given forest area poor sites have merely reduced versions of richer ones. In areas where a greater altitudinal range is sampled, this not the case, with some species being restricted to higher or lower altitudes (Stanisic 1982, Tattersfield et al., 2006). Hence, the inclusion of poorer forest types in some but not all of our regional comparisons does not invalidate the estimation of faunal similarities and turnover.

Faunal Turnover and Taxonomic Composition

There is a considerable amount of faunal turnover over the approximately 550 km distance between our most distant sites. Table 7 demonstrates this by comparison with non-limestone regions along the USA-Canada border (Nekola, 2005, and unpublished), the Sudetes-Carpathian chain in southern Poland (Pokryszko & Cameron, 2005, and unpub-

lished), and the southern Rocky Mountain cordillera in the southwestern USA (Nekola, unpublished). Except for Brisbane, rates of uniqueness in the local eastern Australian faunas were greater than 40%. Outside of eastern Australia, only one other region, the Chiricahua Mountains (Arizona), exceeded this level. All remaining sites demonstrated uniqueness levels < 20%. Given the continuous nature of compositional turnover (Whittaker, 1975; Nekola & White, 1999), the arbitrary transect endpoints should harbour the most unique species, as was observed in eastern Australia, Poland, and the southern Rockies. The higher rates of unique species in the centre of the northeastern USA transect is due to the incursion of southern species into buffered regional climates adjacent to, or immediately downwind of the Great Lakes.

The Nei endpoint similarity was also much lower for the eastern Australian transect (16.3) than for either of the mountain transects (southern Rockies = 41.7, Carpathians = 46.7) or for the northeastern USA (81.3). Assuming that similarity falls in a constant exponential fashion with interregional distance (Nekola & White, 1999), these values indicate that only 190 km is required for faunistic similarity to fall by 50% in eastern Australia, while it will

TABLE 7. Comparative data on turnover and faunal differences for four sets of sites on non-calcareous soils in E. Australia, NE USA, Poland, and SW USA (see text). Kempsey data exclude sites on limestone. The NE USA and Polish sequences run from west to east, the Australian and SE USA from north to south. The Nei ends column gives the value of the Nei index between the two faunas at the ends of each sequence, which are about 500 km distant except in the NE USA where they are 1,800 km apart.

E. Australia	<i>Kenilworth</i>	<i>Brisbane</i>	<i>Lamington</i>	<i>Kempsey</i>	Nei, ends
No. of species	49	34	41	38	16.3
Unique	20	4	18	26	
% Unique	40.8	11.8	43.9	68.4	
NE USA	<i>Duluth, MN</i>	<i>Copper Harbor, MI</i>	<i>Northern Vermont</i>	<i>Northern Maine</i>	Nei, ends
No. of species	23	33	29	19	81.3
Unique	0	6	2	0	
% Unique	0	18.2	6.9	0	
Poland	<i>Mysliborski</i>	<i>Mlynowiec</i>	<i>Podlipowiec</i>	<i>Ustrzyki</i>	Nei, ends
No. of species	37	37	48	46	46.7
Unique	7	4	5	9	
% Unique	18.9	10.8	10.4	19.7	
SW USA	<i>Chiricahua Mts.</i>	<i>Sierra Blanca Mts.</i>	<i>Southern Sangre de Christo Mts.</i>	<i>San Juan Mts.</i>	Nei, ends
No. of species	25	18	20	23	41.7
Unique	12	2	3	4	
% Unique	48.0	11.1	15.0	17.4	

take 400 km in the southern Rockies, 450 km in the Polish Carpathians, and 6,000 km in the northeastern USA. The eastern Australian fauna is thus experiencing geographic turnover at 2.1–31.6 times the rate experienced by these other faunas, helping explain how the outlying Glenugie and Iluka sites demonstrate such high degrees of uniqueness: in eastern Australia the similarity of regions separated by only 100 km would be expected to fall by 30%.

The Australian situation is similar, though not as extreme, as that reported by Tattersfield (1998) and Tattersfield et al. (1998) for Indian Ocean coastal forests and Eastern Arc Mountains in East Africa. In eastern Australia, single-site endemics are unusual except for isolated limestone outcrops (Stanisic & Ponder, 2004). Most species for which we have reliable information have linear ranges between 50 and 200 km (Stanisic, 1990), and these are not always coherent. In this respect, these faunas resemble those of North Island, New Zealand (Barker, 2005), and are very different from those in the semi-arid northwest of Australia, where large camaenid snails often have very restricted ranges (of the order of 1–10 km), and show strict patterns of within-genus allopatric replacement (Solem, 1988; Cameron et al., 2005). Although camaenids and other large-shelled families (Rhytididae and Helicarionidae) do contribute to faunal differentiation in E. Australian forests, it is clear that the much smaller, litter-dwelling Charopidae contribute most, as they do in New Zealand. In Europe and North America small litter dwelling species tend to unify the composition between regions as they have large geographical ranges (Pokryszko & Cameron, 2005). However, in these regions it is generally the large helicoids and clausiliids (Europe) and large polygyrids, endodontids, and helminthoglyptids (North America) that differentiate faunas.

In terms of taxonomic composition, we note that introduced species are only a small element of these faunas, and the few species involved are not usually abundant. While many of the faunas we have examined may be affected by human activities, they have so far retained their integrity as indigenous assemblages.

Pattern and Process

Although interpretation is complicated by sampling errors in many studies (including this one) certain patterns can be discerned and reasonably attributed to known environmen-

tal fluctuations that have influenced the degree of habitat connectedness. In both N.W. Australia and eastern Africa, climatic fluctuations within the Pliocene/Pleistocene have periodically isolated favourable forest habitats, within which stenotypic species have been confined and differentiated (Cameron, 1992; Tattersfield, 1998). Similar proliferation of allopatric sister species occurs elsewhere, for example in the Aegean region of Europe (Douris et al., 1998; Parmakelis et al., 2005). In eastern Australia, periodic isolation of mesic forest habitats during the Pleistocene (Kershaw, 1981, 1994; Lloyd & Kershaw, 1997; Harle, 1997) has constantly altered the extent and connectedness of forest types. While allopatric speciation can be pronounced on isolated limestone outcrops (Stanisic & Ponder, 2004), as in New Zealand (Barker, 2005), few examples of strict allopatry or parapatry between congeners are apparent, especially among the speciose charopids. The presence of co-existing congeners in eastern Australia thus suggests that speciation occurred within small regions, as has been suggested in eastern Africa (Tattersfield, 1998). The presence of altitudinal zonation in the eastern Australian fauna (i.e., Bellenden Ker, Stanisic, 1982) also suggests that some speciation has been driven, as in Africa (Seddon et al., 2005), by topographic complexity.

When considering the very high local diversity of some New Zealand sites, also dominated by small charopids and punctids, Solem (1983, 1984) suggested that this diversity had built up slowly in a very stable environment. By implication, this process involved isolation by distance (which can be modest, given their low mobility), differentiation, and back colonisation into ancestral territory that was still occupied. This process implies that competitive exclusion is relatively unimportant, and that even nearby populations may be sufficiently isolated to allow for differentiation. With the evidence of competitive exclusion in land molluscs being meagre, it is worth noting that a metapopulation structure involving small, temporary and shifting populations allows local co-existence of ecological equivalents (Hubbell, 2001). These dynamics may be important for some tropical and subtropical faunas that consist of low-density populations that are patchily distributed around temporarily favourable microhabitats, such as coarse woody debris (Cameron et al., 2003). As with estimates of local richness, further investigation of such mechanisms will encounter formi-

dable sampling problems. While this current study certainly does not overcome these problems, the data it generated do not contradict the expected patterns generated by these processes.

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APPENDIX 1

Species recorded by Stanisic (1997) in the Macleay Valley, ordered by overall frequency of occurrence, and showing the number of sites occupied in each habitat. For abbreviations, see text. Asterisked species are introduced.

Species	Sites	SF	TRF	LO	DRF	CRF	TOTAL
		17	22	9	15	6	69
<i>Gyrocochlea planorbis</i>		7	13	8	6	5	39
<i>Saladelos macquariensis</i>		5	5	7	10	3	30
<i>Austrochloritis nambucca</i>		6	11	3	3	6	29
Rhytididae MV3		4	9	7	4	2	26
Rhytididae MV7		1	10	3	6	3	23
<i>Thersites novaehollandiae</i>		2	7	4	7	1	21
<i>Coenocharopa multiradiata</i>		0	4	7	9	1	21
<i>Pleuropoma jana</i>		0	1	9	7	3	20
Helicarionidae MV5		5	1	8	3	3	20
<i>Nitor medioximus</i>		0	3	3	10	3	19
Punctidae MV1		0	1	8	5	1	15
Rhytididae MV1		0	2	5	5	3	15
<i>Hedleyella falconeri</i>		0	13	1	1	0	15
<i>Lotula microcosmos</i>		0	2	7	4	1	14
Charopidae MV35		2	3	0	7	2	14
<i>Parmavitrina planilabris</i>		1	8	1	4	0	14

(continues)

(continued)

Species	Sites	SF	TRF	LO	DRF	CRF	TOTAL
		17	22	9	15	6	69
Helicarionidae MV1		1	5	2	6	0	14
<i>Allocharopa belli</i>		1	10	0	2	0	13
<i>Tornatellinops jacksonensis</i>		0	1	9	3	0	13
Charopidae MV33		2	4	3	2	2	13
<i>Pupisoma circumlitum</i>		0	0	8	4	0	12
Pupillid MV1		0	1	7	4	0	12
<i>Hedleyoconcha delta</i>		0	3	3	3	3	12
* <i>Discocharopa aperta</i>		0	0	8	2	1	11
Charopidae MV30		0	0	6	4	0	10
<i>Gastrocopta bifurcata</i>		0	0	7	3	0	10
Charopidae MV22		2	1	4	1	2	10
Camaenidae MV2		3	0	5	0	2	10
<i>Tornatellinops pressus</i>		0	0	5	2	2	9
<i>Cralopa stroudensis</i>		1	2	2	4	0	9
Charopidae MV6		0	0	4	2	2	8
<i>Georissa laseroni</i>		0	0	8	0	0	8
Charopidae MV4		0	0	6	2	0	8
Charopidae MV23		0	0	3	5	0	8
Helicarionidae MV4		1	7	0	0	0	8
<i>Gastrocopta queenslandica</i>		0	0	5	2	0	7
<i>Rhophodon kempseyensis</i>		0	0	7	0	0	7
Camaenidae MV9		4	0	0	2	1	7
<i>Glyptopupoides egregia</i>		0	0	4	2	0	6
<i>Pygmipanda atomata</i>		1	4	1	0	0	6
<i>Coneuplecta calculosa</i>		0	1	2	3	0	6
Camaenidae MV11		1	0	3	2	0	6
<i>Elasmias wakefieldiae</i>		0	0	3	0	2	5
<i>Triboniophora graeffei</i>		1	0	1	1	2	5
Rhytididae MV2		0	3	2	0	0	5
Charopidae MV25		0	1	4	0	0	5
Charopidae MV38		1	3	0	1	0	5
Helicarionidae MV2		0	0	4	1	0	5
Camaenidae MV4		3	0	0	2	0	5
Camaenidae MV7		0	1	1	3	0	5
Cystopeltidae MV1		1	1	0	2	0	4
Charopidae MV7		0	0	4	0	0	4
Charopidae MV24		0	0	1	3	0	4
Charopidae MV27		0	4	0	0	0	4
Charopidae MV31		0	0	2	1	1	4
Charopidae MV46		0	0	4	0	0	4
<i>Posorites conscendens</i>		0	1	2	1	0	4
Camaenidae MV8		1	0	3	0	0	4
Camaenidae MV12		0	0	0	4	0	4
Charopidae MV18		0	2	1	0	0	3
Charopidae MV2		0	0	0	3	0	3
Charopidae MV16		0	0	1	2	0	3
Charopidae MV36		1	2	0	0	0	3
Helicarionidae MV3		0	1	0	2	0	3

(continues)

(continued)

Species	Sites	SF 17	TRF 22	LO 9	DRF 15	CRF 6	TOTAL 69
Camaenidae MV5		0	3	0	0	0	3
Camaenidae MV6		0	0	1	2	0	3
Camaenidae MV10		0	1	2	0	0	3
<i>Gastrocopta pediculus</i>		0	0	2	0	0	2
* <i>Paralaoma caputspinulae</i>		0	0	2	0	0	2
Rhytididae MV4		0	0	0	2	0	2
<i>Ngairea dorrigoensis</i>		0	2	0	0	0	2
<i>Letomola contortus</i>		0	0	2	0	0	2
Charopidae MV1		0	0	2	0	0	2
Charopidae MV9		0	1	0	1	0	2
Charopidae MV13		0	0	2	0	0	2
Charopidae MV26		0	1	1	0	0	2
Charopidae MV34		0	2	0	0	0	2
Charopidae MV40		0	0	0	2	0	2
Charopidae MV44		0	2	0	0	0	2
<i>Liardetia scandens</i>		0	0	1	0	1	2
<i>Austrochloritis brevipila</i>		0	2	0	0	0	2
Camaenidae MV3		2	0	0	0	0	2
* <i>Bradybaena similaris</i>		0	0	1	1	0	2
<i>Cylindrovertilla kingi</i>		0	0	1	0	0	1
Pupillid MV2		0	0	1	0	0	1
* <i>Lamellaxis clavulinus</i>		0	0	0	1	0	1
Succineidae MV1		0	0	1	0	0	1
Rhytididae MV6		1	0	0	0	0	1
<i>Coenocharopa yessabahensis</i>		0	0	1	0	0	1
<i>Egilomen lirata</i>		0	1	0	0	0	1
Charopidae MV3		0	1	0	0	0	1
Charopidae MV5		0	0	1	0	0	1
Charopidae MV8		0	0	1	0	0	1
Charopidae MV10		0	0	0	1	0	1
Charopidae MV11		0	0	0	1	0	1
Charopidae MV12		0	0	0	0	1	1
Charopidae MV14		0	0	1	0	0	1
Charopidae MV15		0	0	0	1	0	1
Charopidae MV19		0	1	0	0	0	1
Charopidae MV20		0	1	0	0	0	1
Charopidae MV28		0	0	1	0	0	1
Charopidae MV29		0	0	0	1	0	1
Charopidae MV32		0	1	0	0	0	1
Charopidae MV37		0	1	0	0	0	1
Charopidae MV39		0	1	0	0	0	1
Charopidae MV41		0	1	0	0	0	1
Charopidae MV42		0	1	0	0	0	1
Charopidae MV43		0	1	0	0	0	1
Charopidae MV45		0	0	1	0	0	1
<i>Papuexul bidwilli</i>		0	0	0	1	0	1
Camaenidae MV1		1	0	0	0	0	1
* <i>Zonitoides arboreus</i>		0	0	0	1	0	1
Total Species		28	55	71	62	27	112

APPENDIX 2

Occurrence of species in each area sampled in 2004. Asterisked species are introduced.

	Kenilworth	Brisbane	Lamington	Glenugie	Iluka	Kempsey
<i>Georissa laseroni</i>	0	0	0	0	0	X
<i>Pleuropoma jana</i>	0	0	0	0	0	X
<i>Pleuropoma draytonensis</i>	X	X	X	0	0	0
<i>Pupina wilcoxi</i>	X	0	0	0	0	0
<i>Pupina strangei</i>	X	0	0	0	0	0
Pupinidae NN1	0	0	0	X	0	0
Pupinidae BR1	X	0	0	0	0	0
<i>Pupinella costata</i>	X	0	0	0	0	0
<i>Velepallina strangei</i>	0	0	X	0	0	0
<i>Tornatellinops jacksonensis</i>	0	X	0	X	X	X
<i>Tornatellinops pressus</i>	0	0	0	0	0	X
<i>Elasmias wekefieldiae</i>	0	0	0	0	0	X
<i>Cylindrovertilla kingi</i>	0	0	0	0	0	X
<i>Glyptopupoides egregia</i>	0	0	0	0	0	X
<i>Gastrocopta pediculus</i>	0	0	0	0	0	X
<i>Gastrocopta bifurcata</i>	X	0	0	0	X	X
<i>Pupisoma circumlitum</i>	X	0	0	X	0	X
<i>Pupisoma porti</i>	X	0	X	0	0	X
Pupillidae MV1	X	X	0	0	0	X
Pupillidae MV2	X	0	0	0	0	0
* <i>Lamellaxis clavulinus</i>	X	0	0	0	0	0
* <i>Lamellaxis gracilis</i>	X	0	0	0	X	0
<i>Strangesta ramsayi</i>	0	X	X	0	0	0
<i>Strangesta assimilans</i>	0	0	0	X	0	0
<i>Strangesta bullacea</i>	0	0	0	0	X	0
<i>Echotrifa strangeoides</i>	X	X	X	0	0	0
<i>Saladelos macquariensis</i>	0	0	0	0	0	X
<i>Saladelos urarensis</i>	0	0	0	X	0	0
Rhytididae MV1	0	0	0	0	0	X
Rhytididae MV2	0	0	0	0	0	X
Rhytididae MV3	X	X	X	0	0	X
Rhytididae MV7	0	0	0	0	0	X
Rhytididae NN1	0	0	0	X	0	0
Rhytididae BR1	X	X	X	0	0	0
Rhytididae SQ5	X	X	0	0	0	0
<i>Hedleyella falconeri</i>	0	X	X	0	0	X
<i>Hedleyella maconelli</i>	X	0	0	0	0	0
<i>Brazieresta larreyi</i>	0	0	0	0	0	X
<i>Pedinogyra rotabilis</i>	0	X	X	0	0	0
<i>Lotula microcosmos</i>	X	X	X	X	X	X
* <i>Paralaoma caputspinulae</i>	0	0	0	0	0	X
Punctidae MV1	0	0	X	0	0	0
<i>Ngairea corticicola</i>	0	0	X	0	0	0
<i>Setomedea seticostata</i>	0	X	X	0	0	0
<i>Mussonula verax</i>	X	X	0	0	0	0
<i>Nautiliropa omicron</i>	X	X	X	0	0	0
<i>Hedleyoconcha delta</i>	0	0	X	0	0	X
<i>Gyrocochlea vinitincta</i>	0	0	X	0	0	0
<i>Gyrocochlea convoluta</i>	0	0	X	0	0	0

(continues)

(continued)

	Kenilworth	Brisbane	Lamington	Glenugie	Iluka	Kempsey
<i>Gyrocochlea cinnamea</i>	X	0	0	0	0	0
<i>Gyrocochlea planorbis</i>	0	0	0	0	0	X
<i>Coenocharopa multiradiata</i>	0	X	0	X	0	X
<i>Coenocharopa sordidus</i>	X	X	0	0	0	0
<i>Coenocharopa parvicostata</i>	X	X	0	0	0	0
<i>Coenocharopa macromphala</i>	X	0	0	0	0	0
<i>Coenocharopa yessabahensis</i>	0	0	0	0	0	X
<i>Rotacharopa densilamellata</i>	X	X	0	0	0	0
<i>Allocharopa belli</i>	X	0	X	0	0	X
<i>*Discocharopa aperta</i>	X	0	0	0	X	X
<i>Egilomen globosa</i>	X	0	0	0	0	0
<i>Egilomen lirata</i>	0	0	0	0	0	X
<i>Elsothera genithecata</i>	0	0	X	0	0	0
<i>Elsothera nautilodea</i>	0	0	0	X	0	0
<i>Letomola contortus</i>	0	0	0	0	0	X
<i>Rhophodon kempseyensis</i>	0	0	0	0	0	X
<i>Rhophodon minutissimus</i>	X	0	0	0	0	0
<i>Rhophodon colmani</i>	X	0	0	0	0	0
<i>Omphaloropa varicosa</i>	X	0	0	0	0	0
species 1 indet.	0	X	0	0	0	0
Charopidae BR2	0	0	X	0	0	0
Charopidae BR11	X	0	0	0	0	0
Charopidae BR13	0	0	X	0	0	0
Charopidae BR15	0	0	X	0	0	0
Charopidae BR22	0	X	X	0	0	0
Charopidae BR23	0	X	0	0	0	0
Charopidae BR28	X	X	0	0	0	0
Charopidae BR29	0	X	0	0	0	0
Charopidae BR30	X	0	0	0	0	0
Charopidae BR31	X	0	0	0	0	0
Charopidae BB39	X	0	X	0	0	0
Charopidae BR41	0	0	X	0	0	0
Charopidae BR42	0	0	X	0	0	0
Charopidae BR43	0	0	X	0	0	0
Charopidae NN6	0	0	0	X	X	0
Charopidae NN7	0	0	0	X	0	0
Charopidae NN8	0	0	0	0	X	0
Charopidae NN17	0	0	0	X	0	0
Charopidae MV1	0	0	0	0	0	X
Charopidae MV3	0	0	0	0	0	X
Charopidae MV4	0	0	0	0	0	X
Charopidae MV7	0	0	0	0	0	X
Charopidae MV8	0	0	0	0	0	X
Charopidae MV11	0	0	0	0	0	X
Charopidae MV12	0	0	0	0	0	X
Charopidae MV13	0	0	0	0	0	X
Charopidae MV14	0	0	0	0	0	X
Charopidae MV16	0	0	0	0	0	X
Charopidae MV22	0	0	0	0	0	X
Charopidae MV24	0	0	0	0	0	x
Charopidae MV25	0	0	0	0	0	X

(continues)

(continued)

	Kenilworth	Brisbane	Lamington	Glenugie	Iluka	Kempsey
Charopidae MV26	0	0	0	0	0	X
Charopidae MV29	0	0	0	0	0	X
Charopidae MV30	0	0	0	0	0	X
Charopidae MV31	0	0	0	0	0	X
Charopidae MV35	0	0	0	0	0	X
Charopidae MV46	0	0	0	0	0	X
Charopidae NE3	0	0	0	0	0	X
Charopidae SQ4	X	0	0	0	0	0
<i>Fastosarion aquila</i>	X	X	X	0	0	0
<i>Parmavitrina planilabris</i>	0	0	0	0	0	X
<i>Nitor medioximus</i>	0	0	0	0	0	X
<i>Nitor pudibunda</i>	X	X	X	0	0	0
<i>Nitor subrugata</i>	0	0	X	0	0	0
<i>Nitor graftonensis</i>	0	0	0	0	X	0
<i>Liardetia scandens</i>	X	0	0	0	0	X
<i>Coneuplecta calculosa</i>	X	X	X	X	0	X
<i>Tarocystis responsivus</i>	X	0	0	0	0	0
species 2 indet.	0	X	0	0	0	0
Helicarionidae MV1	0	0	0	0	0	X
Helicarionidae MV2	0	0	0	0	0	X
Helicarionidae MV3	0	0	0	0	0	X
Helicarionidae MV4	0	0	0	0	0	X
Helicarionidae MV5	0	0	0	0	0	X
Helicarionidae NN5	0	0	0	X	0	0
Helicarionidae NN10	0	0	0	X	0	0
Helicarionidae BR1	0	0	X	0	0	0
Helicarionidae BR5	X	X	X	0	0	0
Helicarionidae BR7	X	X	0	0	0	0
Helicarionidae BR9	0	0	X	0	0	0
<i>*Zonitoides arboreus</i>	0	0	0	0	X	0
<i>*Bradybaena similaris</i>	0	0	0	0	0	X
<i>Sphaerospira fraseri</i>	X	X	X	X	0	0
<i>Thersites novaehollandiae</i>	0	0	0	0	0	X
<i>Thersites richmondiana</i>	0	X	X	0	0	0
<i>Papuexul bidwilli</i>	X	0	0	0	0	0
<i>Posorites turneri</i>	0	0	X	0	0	0
<i>Posorites conscendens</i>	0	X	X	0	0	X
<i>Ramogenia challengerii</i>	X	X	X	0	0	0
<i>Austrochloritis separanda</i>	X	0	0	0	0	0
<i>Austrochloritis porteri</i>	0	0	X	0	0	0
<i>Austrochloritis nambucca</i>	0	0	0	0	0	X
Camaenidae SQ2	X	X	0	0	0	0
Camaenidae BR1	0	0	X	0	0	0
Camaenidae NN1	0	0	0	X	0	0
Camaenidae NN2	0	0	0	0	X	0
Camaenidae MV4	0	0	0	0	0	X
Camaenidae MV6	0	0	0	0	0	X
Camaenidae MV10	0	0	0	0	0	X
Camaenidae MV11	0	0	0	0	0	X
total	49	34	41	17	11	67
unique	20	4	18	10	5	52
% unique	40.82	11.76	43.9	58.82	45.45	77.61